The influence of aquaculture unit proximity on the pattern of *Lepeophtheirus salmonis* infection of anadromous *Salmo trutta* populations on the Isle of Skye, Scotland

I. MOORE[1*], J.A. DODD[1,2], M. NEWTON[3], C.W. BEAN[1], I. LINDSAY[4], P. JAROSZ[4] AND C.E. ADAMS[1]

[1] *Scottish Centre for Ecology and the Natural Environment, University of Glasgow, Rowardennan, G63 0AW, U.K.,* [2] *Veritas Ecology Limited, 6 Forest Cottage, Rowardennan, Stirlingshire, G63 0AW, U.K.,* [3] *Atlantic Salmon Trust, 11 Rutland Square, Edinburgh, EH1 2AS, U.K. and* [4] *Skye and Wester Ross Fisheries Trust, Harbour Centre, Gairloch, IV21 2BQ, U.K.*

* Author to whom correspondence should be addressed. Tel.: +44 1360 870510; email: isabelmoore89@gmail.com

A total of 230 anadromous *Salmo trutta* (brown trout) were sampled in five sheltered coastal fjords (or sea lochs) on the Isle of Skye, Scotland, U.K., in 2016 at varying distances from active Atlantic salmon *Salmo salar* farms. Statistical models were developed to investigate potential correlations between salmon lice *Lepeophtheirus salmonis* burdens on *S. trutta* hosts and their proximity to *S. salar* farm cages. Significant correlations were found between lice burdens and fish fork length and proximity to the nearest *S. salar* farm. The probability of the presence of *L. salmonis* on fish hosts increased with fish host size and with distance from the nearest *S. salar* farm, but total lice burdens were highest in fish sampled near *S. salar* farms

This article has been accepted for publication in the *Journal of Fish Biology* and undergone full peer review but has not been through the copyediting, typesetting, pagination and proofreading process, which may lead to differences between this version and the Version of Record. Please cite this article as doi: 10.1111/jfb.13625

and decreased with distance. The proportion of different life-cycle stages of *L. salmonis* were also dependent on *S. salar* farm proximity, with higher juvenile lice numbers recorded at sites near *S. salar* farm cages. These results highlight the complexity of the relationship between *S. trutta* and *L. salmonis* infections on wild fish and emphasise the requirement of further research to quantify these effects to better inform conservation and management strategies, particularly in areas of active *S. salar* farm facilities.

Key words: coastal zone; dispersion; *Lepeophtheirus salmonis*; lice parasite; *Salmo salar*; salmonid

INTRODUCTION

Migration, the spatial movement of an animal to and from a specific area, is commonly exhibited by a wide variety of different taxa (Bohlin *et al*., 2001; Acolas *et al*., 2008; Chapman *et al*., 2011). The benefits that may arise from migration include greater access to resources, which frequently result in increased growth rate and fecundity (Eldøy *et al*., 2015). Large scale movements are exhibited by diadromous salmonids, such as brown trout *Salmo trutta* L. 1758 and Atlantic salmon *Salmo salar* L. 1758. Following a variable time period in fresh water, a subset of most *S. trutta* populations will smolt and undertake a seaward migration (Jonsson & Jonsson, 2011; Thorstad *et al*., 2016). This enigmatic behaviour is thought to occur only when the benefits of the migration (increased resources, fecundity *etc*.) outweigh the costs (increased predation, exposure to disease *etc*.) to the individual in the marine environment (Bohlin *et al*., 2001; Jonsson & Jonsson, 2011; Thorstad *et al*., 2016).

There is strong evidence that salmonid populations are in decline in many areas, including the U.K., Europe and Canada (Ford & Myers, 2008; Middlemas *et al*., 2013; Thorstad *et al*., 2015). Although this trend is difficult to quantify because of the logistical problems associated with sampling fish populations that travel such large distances (ICES, 2017*a*), it is apparent in rivers with long term count data, as well as in those with historic rod catch records (Gross *et al*., 1988; Gjelland *et al*., 2014; Gauld *et al*., 2016; ICES 2017*b*). As a result of its cultural and economic importance considerable previous research has focussed on the challenges facing *S. salar* populations (Limburg & Waldman, 2009). In contrast, considerably less attention has been given to the causes of decline of *S. trutta* (Drenner *et al*., 2012; Eldøy *et al*., 2017, Glover *et al*., 2017).

It is well established that, during the marine stage of their life cycle, anadromous *S. trutta* gain benefits from access to increased resources, but they are also exposed to increased

costs, such as disease and predation, which can result in high levels of mortality (Drenner *et al*., 2012; Gjelland *et al*., 2014). Thus, any change to the relative costs and benefits of marine migration have the potential for significant effects on anadromous populations. This has led to speculation that changes in marine migration costs might be contributing to the decline in anadromous *S. trutta* (Gjelland *et al*., 2014; Jennings *et al*., 2016).

One suspected contributing source of mortality that may have increased in recent years is the potential for infestation by *Lepeophtheirus salmonis*, a naturally occurring sea louse parasite that feeds on the mucus, tissue and blood of their hosts, primarily salmonids (Boxaspen, 2006; Fast *et al*., 2007; Thorstad *et al*., 2015). The complex *L. salmonis* life cycle can be divided into eight developmental stages: two larval napulii phases that are planktonic, one copepodite phase that is also planktonic and free floating but must attach to a host, two chalimus phases (when the lice are able to begin feeding on their host), two pre-adult phases and a final mature or reproductive phase (Fast *et al*., 2007; Gjelland *et al*., 2014; Thorstad *et al*., 2015). Beginning at the pre-adult phases, *L. salmonis* are able to move on the body surface of their host and can actively swim for short distances (Thorstad *et al*., 2015). The planktonic stages can be carried by wind-driven and tidal currents (Costello, 2009; Asplin *et al.,* 2014).

High *L. salmonis* burdens can lead to increased osmoregulatory stress and eventual mortality in salmonids (Middlemas *et al*., 2013; Taranger *et al*., 2015; Thorstad *et al*., 2015). The incidence of *L. salmonis* on wild salmonids has increased since the 1960s and has been linked with the development of commercial *S. salar* farming (Thorstad *et al*., 2015).

In 2016, the international commercial aquaculture industry produced 1.5 Mt of *S. salar* and the industry has continued to grow (OECD, 2018). Previous research has suggested that expanding coastal *S. salar* farming in the U.K., Norway and Canada could lead to an

increase in the densities of infective *L. salmonis* in coastal areas (Boxaspen, 2006; Gargan *et al*., 2012; Thorstad *et al*., 2015; Arechavala-Lopez *et al*., 2016; Shephard *et al*., 2016).

The observed increase in densities of infective *L. salmonis* on wild *S. trutta* populations has been linked with high densities of *S. salar* in marine farm cages, which provide *L. salmonis* with a large, easily accessible population of host species and allow them to feed and reproduce successfully if left untreated (Salama *et al*., 2013). Open-net cages allow for the dispersion of free-floating *L. salmonis* from the cages and into the surrounding area, thus increasing their abundance in the surrounding ecosystem (Amundrud & Murray, 2009).

Coastal zones, frequently used for rearing *S. salar* in cages particularly in western Norway and Scotland, are also important feeding grounds for migratory *S. trutta* post-smolts (Jonsson & Jonsson, 2011). This habitat overlap has the potential to expose individual wild *S. trutta* to unnaturally elevated levels of *L. salmonis* parasites and could thus lead to higher than natural lice infestations (Costello, 2009; Asplin *et al.,* 2014; Thorstad *et al*., 2015; Gargan *et al.* 2012).

Research in Scandinavia, North America and the U.K. has demonstrated that in areas where *S. salar* farms are present, a higher abundance of lice can be found in the water column and that wild salmonids are more heavily infected by *L. salmonis* (Gargan *et al.*, 2012; Rees *et al.,* 2015; Thorstad *et al*., 2015). Similar trends have been observed in local salmonid populations on the west coast of Scotland. In a study in Loch Torridon, Penston & Davis (2009) reported that the number of gravid *L. salmonis* found on farmed *S. salar* was 'significantly correlated with the densities of *L. salmonis* copepodites in the water column'. Middlemas *et al.* (2013) reported that the proportion of wild *S. trutta* with high *L. salmonis* infestations was significantly correlated to proximity of individual hosts to *S. salar* farms and to fish length across the west coast of Scotland. Similarly, Shephard *et al.* (2016) showed that

higher levels of *L. salmonis* infection were more commonly found on *S. trutta* which were captured closer to *S. salar* farm cages in Scotland and Ireland. Although knowledge of the dispersion rates and transmission locations of *L. salmonis* populations to wild salmonids is improving, there is still an urgent need for more information on the infection rates of *L. salmonis* in wild *S. trutta* in near-shore coastal habitats to provide further insight into the effects of *S. salar* aquaculture on wild salmonid populations in Scotland (Middlemas *et al.*, 2013).

Commercial *S. salar* farming began in Scotland in the 1960s and has continued to expand over time on its northern and western coasts (Ellis *et al.*, 2016). In 2016, 162 817 t of farmed *S. salar* were produced in Scotland and valued just below £600 million sterling (Kenyon & Davies, 2018). The Scottish Government is encouraging the growth of the industry, hoping to increase production to 210 000 t by 2020 (Kenyon & Davies, 2018). This continued expansion of the industry suggests that wild *S. trutta* populations in Scotland may face increased pathogen exposure as more *S. salar* farms are established.

Currently, the Isle of Skye (57^{o} 25′ N; 6^{o} 20′ W) on the west coast of Scotland supports over ten active *S. salar* farms and several inactive, or fallow, farms that have previously been in use. With the continued future expansion of both the production capacity of current *S. salar* farms and the number of active farm sites around the island, it is crucial to gain a better understanding of salmonid behaviour in these shared habitats, as well as the effects of *L. salmonis* infection burdens on an already declining wild *S. trutta* population.

Using anadromous *S. trutta* populations that were captured in five sheltered coastal inlets (hereafter referred to as sea lochs) on the Isle of Skye (Fig. 1), the relationships between *L. salmonis* burdens on individual fish hosts and sampling site proximity to active *S. salar* farms were investigated.

MATERIALS AND METHODS

SAMPLING

Five sea lochs, located around the Isle of Skye (Loch Snizort, Slapin, Portree, Eishort and Harport) were sampled between April and September 2016 (Fig 1 and Table I). The sites varied in their distance from active *S. salar* farms from 3 km (Loch Portree) to 48 km (Loch Eishort). All *S. trutta* were caught using a combination of seine and fyke netting techniques in the tidal zones of each sea loch. The netting method used was dependent on site accessibility. Seine netting was carried out at Loch Slapin and Snizort on a falling tide. A seine net of 30 m length and 20 mm mesh size was used at Loch Slapin and one of 50 m length and 20 mm mesh size was used at Loch Snizort. All captured fish were recovered with a large hand net and placed into a holding tank for processing.

In Loch Portree, Eishort and Harport, two fyke nets (14 mm mesh size) were set in the mouth of the principal river discharging into the loch, with one net placed in a downstream and one in an upstream facing direction. Leader nets were stretched to either bank to increase the chances of intercepting moving fish and guiding them into the net. The fyke nets were left in position for between 2 and 4 days and checked every 12 hours on a low tide. Any fish captured was placed into a holding tank for processing.

All captured fish were anesthetised using MS-222 and their mass (M, g) and fork length (L_F, mm) were measured. From these, Fulton's condition factor ($K = M\,L_F^{-3}$) (Fulton, 1904; Nash *et al.* 2006) was calculated. Visual *L. salmonis* counts were conducted on each fish and the number of *L. salmonis* at each life stage (*i.e.* juvenile, mobile and gravid female) was recorded. All *L. salmonis* within the chalimus life stages were classified as juveniles, *L. salmonis* within the pre-adult, mature male and non-gravid female stages were classified as

mobile and reproducing female *L. salmonis* with attached paired egg strings were classified as gravid females. All visual counts were conducted by the same researcher throughout the study to eliminate observer bias. All fish were released back into the site they were captured from after they had sufficiently recovered from the anaesthetic and were able to swim independently.

Using *S. salar* farm locations available from the Scottish Government's aquaculture website (Scottish Government, 2018), the distance by sea from each sampling site to the nearest active farm site was calculated. The Scottish Government defines an active site as 'an aquaculture site that has either actively produced fish or shellfish in the last 3 years or which is fallow as a part of a planned production cycle' (Scottish Government, 2018).

STATISTICAL ANALYSIS

To investigate the relationship between *L. salmonis* burdens on individual *S. trutta* hosts, five models were developed. Firstly, drivers of total *L. salmonis* burden were explored and secondly, drivers of life stage specific *L. salmonis* burden were investigated. R statistical software (www.r-project.org) and packages AICcmodavg (Mazerolle, 2016), effects (Fox, 2003), ggplot2 (Wickham, 2009), glmmADMB (Fournier *et al*., 2012), lattice (Sarkar, 2008), lme4 (Bates *et al*., 2015), multcomp (Hothorn *et al*., 2008), plyr (Wickham, 2011), pscl (Zeileis *et al*., 2008) and R2admb (Bolker *et al.*, 2016) provided the platform for all data analyses.

TOTAL ABUNDANCE OF *L. SALMONIS*

Due to the relatively high numbers of fish that were found to be uninfected by *L. salmonis* (52%), the lice burden on individual *S. trutta* was examined using mixed-effects models designed to handle zero-inflated data, classified as data made up of more than 25% zeros (Jansen *et al*., 2012; Zuur & Ieno, 2016). A binomial mixed-effects model was created using the lmer4 and lattice packages in R to identify the factors that were influencing the presence or absence of *L. salmonis* on *S. trutta.* A second truncated negative binomial mixed effects model was created using the packages R2admb and glmmADMB in R to determine which covariates affect the *L. salmonis* burdens found in the positive non-zero count data of the study.

In both models, the presence or abundance of *L. salmonis* was the primary response variable, while L_F, *S. salar* farm proximity (km), *K* were treated as covariates. A maximum statistical model including all covariates, their interactions and also netting method as a random variable was created. A minimum adequate model was generated by a process of significance testing between models (ANOVA) and the sequential backward elimination of non-significant terms. The final model selected was the simplest model containing only significant predictors of the primary response variable, which was within two units of the lowest AIC value (Zuur & Ieno, 2016).

LIFE STAGE SPECIFIC *L. SALMONIS* BURDEN

Three life-stage specific maximum generalized linear models (GLM) including the covariates and their interactions were created for each of the three broad life stages of *L. salmonis*. The life-stage specific burden of *L. salmonis* (*i.e*. juvenile, mobile and gravid female) was the primary response variables, whilst *S. salar* farm proximity (km) and total *L. salmonis* burden per individual host fish were treated as covariates. The final model for each

life stage was selected using ANOVA significance testing to remove non-significant terms and ultimately determine the simplest model using AIC values. Statistical analysis of this dataset ensured that model assumptions were met and collinearity was checked to identify covariates that were highly correlated. Highly correlated covariates, such as *M*, were removed from further analysis to avoid replication of variation.

RESULTS

A total of 230 fish were sampled from five sites and all results are presented as mean ± S.E. (Table I). Across all sites, *S. trutta* had a mean L_F = of 216.4 ± 4.6 mm and a mean ± total parasite load of 5.6 ± 0.9 *L. salmonis* individuals per fish (Table I). Overall, the mean numbers of juvenile, mobile and gravid female lice per fish were 3.4 ± 0.7, 1.5 ± 0.3 and 0.7 ± 0.1, respectively (Table I).

The binomial mixed-effects model returned significant relationships between the presence of *L. salmonis* on individual *S. trutta* and *S. salar* farm proximity (km) and L_F (Table II). The probability of an individual *S. trutta* being infected with *L. salmonis* was positively related to the distance to an active farm ($P < 0.001$) (Fig. 2). Additionally, the model showed that the probability of *L. salmonis* presence on *S. trutta* was positively correlated to the length of a fish ($P < 0.001$) (Fig. 3). Thus there was a higher probability of finding *L. salmonis* on larger fish and on fish that were further away from a *S. salar* farm. The truncated negative binomial model indicated that *S. trutta* hosts that were infected with *L. salmonis* were more likely to have higher lice burdens in areas nearest to *S. salar* farms and that burden declined with increasing distance from the nearest farm ($P < 0.01$) (Fig. 4).

The three life-stage specific GLM models determined that the proportions of different life stages of *L. salmonis* contributing to the total lice burden on *S. trutta* were significantly influenced by the proximity of sampling sites to the nearest *S. salar* farm (Fig. 5).

JUVENILE LIFE STAGE

The proportion of juvenile *L. salmonis* was significantly influenced by an interaction between the total lice burden of *L. salmonis* on an individual fish and the proximity of the nearest *S. salar* farm ($P < 0.001$) (Fig. 6). This interaction was typified by a relationship where, on fish captured in close proximity to *S. salar* farms and when the lice burden on the fish was high, juvenile lice comprised a low proportion of the total lice burden. This relationship was reversed when total lice burden on fish, captured close to *S. salar* farms, was low; *i.e*. juvenile lice formed a relatively higher proportion of the lice burden. Furthermore, when individual fish were sampled further from *S. salar* farms, the proportion of juveniles would also fluctuate based on the total lice burden of *L. salmonis*. Fish with lower lice burdens would have fewer juvenile lice, while fish with a high lice burden would have a high proportion of juveniles.

MOBILE LIFE STAGE

A significant and positive relationship between the proportion of mobile *L. salmonis* on *S. trutta* hosts and *S. salar* farm proximity was also identified ($P < 0.001$) (Table III). The model results indicated that the proportion of mobile lice contributing to the total lice burden increased with increasing distance from *S. salar* farms.

GRAVID FEMALE LIFE STAGE

The model indicated that individual fish sampled at increasing distances from *S. salar* farms had a higher proportion of gravid *L. salmonis* females ($P < 0.001$) (Table II). Additionally, a significant and negative relationship was found between the proportion of mature gravid females and the total lice burden found on sampled *S. trutta* ($P < 0.001$). This indicated that as the total burden of *L. salmonis* increased, the number of gravid females comprising the total lice burden declined.

DISCUSSION

The probability of finding *L. salmonis* present on a host fish significantly increases with L_F. Larger fish often have higher lice burdens simply due to the increased surface area available to feeding *L. salmonis* (Tucker *et al*., 2002; Costello, 2009; Middlemas *et al.,* 2013) and there is an increased likelihood of *L. salmonis* encountering a fish with a larger surface area. Migratory *S. trutta* occupy coastal areas during the marine phase of their life cycle as they try to maximise individual growth rates. Increases in the amount of time spent in these environments have the potential to amplify the number of encounters an individual fish has with *L. salmonis*, as well as the host's overall louse burden.

The proximity of *S. salar* farms had a significant effect on both the probability of infection with *L. salmonis* and on the total lice burden of infected *S. trutta*. There was a higher probability of finding *L. salmonis* present on *S. trutta* that are further away from the nearest *S. salar* farm. Because *L. salmonis* is a naturally occurring parasite, varying abundances of this ectoparasite can also be found in coastal areas where *S. salar* farms are

not present (Urquhart *et al*., 2010; Jansen *et al*., 2012; Thorstad *et al*., 2015). Large, shallow and sheltered sea lochs that *S. trutta* have been shown to use as feeding grounds are also capable of supporting native *L. salmonis* populations due to the continuous presence of host species utilising the same area (Costello, 2009; Urquhart *et al.,* 2010).

The study sites Loch Slapin and Loch Eishort have similar geographic characteristics (large, shallow and sheltered) and are located 46 and 48 km, respectively, away from the nearest *S. salar* farm. Historically, there was an active *S. salar* farm in Loch Slapin, but the site was closed *c.* 8 years prior to this study due to high levels of lice infestation that the farm operators were unable to control. The farm site has remained fallow ever since and, based on previous studies suggesting that *L. salmonis* levels are significantly reduced after a fallowing period of six months (Bron *et al*., 1993; Rae, 2002; Costello, 2006), it is unlikely that the history of this site would have an effect on the levels of *L. salmonis* observed during this study.

An average of 3.7 ± 0.7 total *L. salmonis* individuals per fish were reported in Loch Slapin in this study and 7.0 ± 2.1 total *L. salmonis* individuals per fish in Loch Eishort. A literature review by Thorstad *et al*. (2015) reported peak natural *L. salmonis* levels in areas without *S. salar* farms as 4–8 lice per individual *S. trutta* in summer and autumn months. Because of this, and the probable favourable environmental conditions for supporting *S. trutta* hosts and their *L. salmonis* populations within Lochs Slapin and Eishort, it is highly possible that for these sites *L. salmonis* densities represent lice levels that would occur naturally without the influence of *S. salar* farms.

In contrast to the high probability of finding one or more *L. salmonis* on *S. trutta* sampled in areas further from *S. salar* farms, higher abundances of *L. salmonis* were found on host individuals that were captured in areas that are geographically closer to *S. salar* farm pens. These findings are similar to those of a number of other studies (Parker & Margolis,

1964; Middlemas *et al.*, 2013; Shephard *et al*., 2016). For example, a modelling study by Gillibrand & Willis (2007) reported a similar result, in that copepodid abundance on wild fish reached a maximum between 7 and 12 km from the *S. salar* farm source. However, the distance at which maximum infection rate occurs will vary depending on topography, wind-driven and tidal currents (Costello 2009).

High lice loading is particularly apparent in Loch Snizort in this study, where an average of 20.5 ± 5.1 *L. salmonis* per fish was recorded and the nearest *S. salar* farm is 13 km away. A burden of *L. salmonis* of this magnitude is thought to have a direct effect on mortality in wild salmonids (Taranger *et al*., 2015). Taranger *et al*. (2015) developed an index to assess *L. salmonis* burdens in relation to fish mass. The index used laboratory experiments to calculate the increased chance of mortality in both post smolts (< 150 g) and larger salmonids (> 150 g) based on the mass of the fish. Their results indicated that post smolts with 0.2–0.3 lice $g^{-1}$of fish and larger salmonids with 0.05–0.10 lice g^{-1} of fish, carried a 50% risk of mortality. Additionally, they determined that if a post smolt had a burden of > 0.3 lice g^{-1} and a larger salmonid had > 0.15 lice g^{-1}, then those individuals had a 100% risk of dying.

The probability model of Taranger *et al*. (2015) has not been tested empirically in a field environment and therefore should not be viewed as a final answer to management questions on the critical loading level of salmonid lice abundance in the wild (Thorstad *et al*., 2015). For example, the average mass of the *S. trutta* sampled in Loch Snizort was 54.1 ± 5.9 g and the average number of *L. salmonis* on each fish was 20.5 ± 5.1, which equates to 0.38 lice g^{-1}. This value exceeds the threshold reported by Taranger *et al*. (2015), which leads to 100% lice related mortality in salmonids of less than 150 g mass. In comparison, fish from Loch Slapin and Loch Eishort, where the nearest *S. salar* farm is more than 45 km away, had respective mean values of 0.02 lice g^{-1} and 0.04 lice g^{-1}, respectively These levels are lower than the threshold predicted by Taranger *et al*. (2015) as increasing the probability of

mortality in fish < 150 g at all, but would, however, result in a 20% lice-related mortality in fish weighing more than 150 g.

LIFE STAGE SPECIFIC *L. SALMONIS* BURDEN

By looking at the life-cycle stages of *L. salmonis* and their relative proportion as a part of the total lice burden, further information about the potential location of parasite transmittance between fish populations emerges. In this study, all stages of the *L. salmonis* life cycle are significantly influenced by the proximity of the sampled host individual to the nearest *S. salar* fish farm. However, differences in this relationship are evident between the proportion of juvenile *L. salmonis* and the proportions of mobile and gravid females that make up the total lice burden.

The relative proportions of juvenile *L. salmonis* consistently make up a large share of the total number of lice on *S. trutta* sampled near to *S. salar* farms, but this ratio fluctuates depending upon the total lice abundance and the host's proximity to a farm. This complex relationship highlights the variation of dispersion rates and distances that juvenile *L. salmonis* may disperse from their source. Previous studies demonstrated that increased *L. salmonis* abundance can be observed up to 30 km away from *S. salar* farms (Middlemas *et al.,* 2013; Rees *et al.,* 2015).

Marine *S. salar* aquaculture production units in Scotland are commonly located in coastal areas, a habitat that is widely used by young smolt and post-smolt *S. trutta* (Shephard *et al*., 2016). The open net pens that are used in these facilities allow free floating *L. salmonis* larvae to disperse from net pens by wind and tidal currents and potentially come into contact with any wild fish in the area (Penston *et al*., 2008, Costello, 2009). Therefore, it could be argued that the habitats frequented by the young fish that were sampled in this study are often

predisposed towards having higher juvenile lice densities because of the presence of *S. salar* farms, which act as a key source of *L. salmonis* larvae (Penston *et al*., 2008; Penston & Davies, 2009; Thorstad *et al*., 2015). Brooks (2005), however, reported a higher probability of finding the infective stages of *L. salmonis* at a distance of 7–10 km from their source (*S. salar* farms) as a result of a combination of the time taken to develop to the infectious stage and dispersion of lice larvae *via* water currents. Thus, local environmental conditions (e.g. salinity, temperature, topography, currents and tides, *etc*.) may all affect probability of infection and infection rate. While the majority of research has demonstrated that the transmission of lice at the juvenile stage is more likely to occur close to the source of the population (*i.e. S. salar* farms), it is possible that, in areas of high louse density, a portion of the lice in their larval stage would be carried away by local environmental conditions before they are developed enough to attach to a host (Brooks & Stucchi, 2006; Penston & Davies, 2009). Several modelling studies have demonstrated that *L. salmonis* dispersion can be explained by wind and tidal currents, which can carry the lice up to 30 km in Scottish loch systems (Krkošek *et al*., 2005; Middlemas *et al*., 2013; Salama *et al*., 2013) and up to 97 km in Norwegian fjords (Asplin *et al*., 2014).

The relationships between the mobile and gravid female life stages are less complex. There is a certain amount of variation between the ratio of each life stage relative to the total burden of lice on an individual fish sampled near a *S. salar* farm. As the distance from the nearest *S. salar* farm increases, however, the proportion of mobile lice also increases. The proportion of gravid females follows a similar trend as it increases with distance from *S. salar* farms. Additionally, the ratio of gravid females is higher on fish with low lice abundance, but decreases slightly when the total lice abundance increases. These trends would suggest that the more mature stages of the *L. salmonis* life cycle comprise a larger proportion of the total lice burden in areas more distant from *S. salar* farms.

The varying ratios of different life stages found across the large spatial area of this study could be explained by the speed of progression through successive life-stage moults, which can occur over a series of weeks or months, depending on climatic conditions (Boxaspen, 2006). *Salmo trutta* sharing coastal habitats with *S. salar* fish farms would be exposed to the juvenile stages of lice in those environments, which would then contribute to the high proportion of juveniles found in the total lice burdens (Penston & Davies, 2009). As infected *S. trutta* are likely to move around coastal areas, as part of their migration strategy, the surviving lice would continue to feed and reach sexual maturity, therefore contributing more mobile lice to the total ratio found on more mature fish that have moved away from the source of infection. However, there are other possible explanations for the observed patterns of life stage *L. salmonis* infections on fish in this study. One possibility is that those fish that acquire the high infection rate documented closer to farm sites may well have a higher probability of dying if juvenile *L. salmonis* develop to the more damaging mobile stages (Thorstad *et al.* 2015). High levels of mortality would not be detected in this study design. Thus, the higher relative ratio of the mobile *L. salmonis* stages further away from farms may represent fish that have been previously subjected to low juvenile *L. salmonis* infection rates that exert a lower mortality rate.

Results from this study have provided further insight into the complex relationships between *S. trutta* and *L. salmonis* populations. As the *S. salar* aquaculture industry continues to expand in Scotland, it is critical to have a better understand of farming interactions, such as disease transfer, with already threatened wild salmonid communities. This study did not include the effects of temperature, current, wind, salinity, or early fresh water entry on *L. salmonis* loading. Additionally, there is little information on the movement of *S. trutta* between sea lochs and the extent of their travel around the coastlines of Scotland. Future work in this field could include the tracking of *S. trutta* movement at varying ages in

combination with modelling *L. salmonis* dispersion rates in Scottish sea lochs to determine the extent of transmission at stages of the *L. salmonis* life cycle in areas with different environmental and climatic factors. Such research would help elucidate the details of *L. salmonis* dispersal mechanisms between farmed and wild salmonid populations. Nevertheless, our data add to the empirical evidence that *L. salmonis* from farms can cause fatal infestations of wild *S. trutta* and highlight the importance of limiting *L. salmonis* abundance on farms to improve wild salmonid survival.

This project was part funded by Grieg Seafood Ltd. Three of the sites in this study were sampled as part of an ongoing *L. salmonis* monitoring project funded by the Scottish Government. We thank the Skye and Wester Ross Fisheries Trust and their numerous volunteers, A. Macaskill and the John Muir Trust, Marine Harvest Scotland and The Scottish Salmon Company for assisting with field work, sample collection and for site access permission. Many thanks also to E. Dickinson, A. Lothian and H. Honkanen for statistical support.

CONTRIBUTIONS

I.M., data generation, data analysis, manuscript preparation; J.A.D., ideas, data analysis, manuscript preparation; M.N., data analysis, manuscript preparation; C.W.B., ideas, manuscript preparation; I. L., ideas, field work support, manuscript preparation, funding; P.J., manuscript preparation, funding; C.E.A., ideas, data analysis, manuscript preparation, funding.

References

Acolas, M., Roussel, J. & Baglinière, J. (2008). Linking migratory patterns and diet to reproductive traits in female brown trout (*Salmo trutta* L.) by means of stable isotope analysis on ova. *Ecology of Freshwater Fish* **17**, 382-393. doi: 10.1111/j.1600-0633.2007.00290.x

Amundrud, T. & Murray, A. (2009). Modelling salmon lice dispersion under varying environmental forcing in a Scottish sea loch. *Journal of Fish Diseases* **32**, 27-44. doi: 10.1111/j.1365-2761.2008.00980.x

Arechavala-Lopez, P., Berg, M. & Finstad, B. (2016). Large-scale use of fish-traps for monitoring sea trout (*Salmo trutta*) and salmon lice (*Lepeophtheirus salmonis*) infestations: efficiency and reliability. *Marine Biology Research* **12**, 76-84. doi: 10.1080/17451000.2015.1069356

Asplin, L., Johnsen, I., Sandvik, A., Albresten, J., Sundfjord, V., Aure, J. & Boxaspen, K. (2014). Dispersion of salmon lice in the Hardangerfjord. *Marine Biology Research* **10**, 215-225. doi: 10.1080/17451000.2013.810755

Bates, D., Maechler, M., Bolker, B. & Walker, S. (2015). Fitting Linear Mixed-Effects Models Using lme4. *Journal of Statistical Software*, **67**, 1-48. doi:10.18637/jss.v067.i01

Bohlin, T., Pettersson, J. & Degerman, E. (2001). Population density of migratory and resident brown trout (*Salmo trutta*) in relation to altitude: evidence for a migration cost. *Journal of Animal Ecology* **70**, 112-121. doi: 10.1046/j.1365-2656.2001.00466.x

Bolker, B., Skaug, H. & Laake, J. (2016). R2admb: 'ADMB' to R Interface Functions. R package version 0.7.15. Available at www.CRAN.R-project.org/package=R2admb

Boxaspen, K. (2006). A review of the biology and genetics of salmon lice. *ICES Journal of Marine Science* **63**, 1304-1316. doi: 10.1016/j.icesjms.2006.04.017

Bron, J., Sommerville, C., Wootten, R. & Rae, G. (1993). Fallowing of marine Atlantic salmon, *Salmo salar* L., farms as a method for the control of sea lice, *Lepeophtheirus salmonis* (Kroyer, 1837). *Journal of Fish Diseases* **16,** 487-493. doi: 10.1111/j.1365-2761.1993.tb00882.x

Brooks, K. (2005). The effects of water temperature, salinity and currents on the survival and distribution of the infective copepodid stage of salmon lice (*Lepeophtheirus salmonis*) originating on Atlantic salmon farms in the Broughton Archipelago of British Columbia. *Reviews in Fisheries Science* **13**, 177-204. doi: 10.1080/10641260500207109

Brooks, K. & Stucchi, D. (2006). The effects of water temperature, salinity and currents on the survival and distribution of the infective copepodid stage of salmon lice (*Lepeophtheirus salmonis*) originating on Atlantic salmon farms in the Broughton

Archipelago of British Columbia – a response to the rebuttal of reviews in Fisheries Science. *Reviews in Fisheries Science* **14**, 13-23. doi: 10.1080/10641260500448893

Chapman, B., Brönmark, C., Nilsson, J. & Hansson, L. (2011). The ecology and evolution of partial migration. *Oikos* **120**, 1764-1775. doi: 10.1111/j.1600-0706.2011.20131.x

Costello, M. (2006). Ecology of sea lice parasitic on farmed and wild fish. *Trends in Parasitology* **22,** 475-483. doi: 10.1016/j.pt.2006.08.006

Costello, M. (2009). How salmon lice from salmon farms may cause wild salmonid declines in Europe and North America and be a threat to fishes elsewhere. *Proceedings of the Royal Society B* **276**, 3385-3394. doi: 10.1098/rspb.2009.0771

Drenner, S., Clark, T., Whitney, C., Martins, E., Cooke, S. & Hinch, S. (2012). A synthesis of tagging studies examining the behaviour and survival of anadromous salmonids in marine environments. *PLoS ONE* **7**, 1-13. doi: 10.1371/journal.pone.0031311

Eldøy, S., Davidsen, J., Thorstad, E., Whoriskey, F., Aarestrup, K., Næsje, T., Rønning, L., Sjursen, A., Rikardsen, A. & Arnekleiv, J. (2015). Marine migration and habitat use of anadromous brown trout (*Salmo trutta*). *Canadian Journal of Fisheries and Aquatic Sciences* **72**, 1366-1378. doi: https://doi.org/10.1139/cjfas-2014-0560

Eldøy, S., Davidsen, J., Thorstad, E., Whoriskey, F., Aarestrup, K., Næsje, T., Rønning, L., Sjursen, A., Rikardsen, A. & Arnekleiv, J. (2017). Marine depth use of sea trout

Salmo trutta in fjord areas of central Norway. *Journal of Fish Biology* **91**, 1268-1283. doi:10.1111/jfb.13463

Ellis, T., Turnbull, J., Knowles, T., Lines, J., Auchterlonie, N. (2016). Trends during development of Scottish salmon farming: An example of sustainable intensification? *Aquaculture* **458,** 82-99. doi:10.1016/j.aquaculture.2016.02.012

Fast, M., Johnson, S., Eddy, T., Pinto, D. & Ross, N. (2007). *Lepeophtheirus salmonis* secretory/excretory products and their effects on Atlantic salmon immune gene regulation. *Parasite Immunology* **29**, 179-189. doi: 10.1111/j.1365-3024.2006.00932.x

Ford, J. & Myers, R. (2008). A global assessment of salmon aquaculture impacts on wild salmonids. *PLoS Biology* **6**, 411-417. doi: 10.1371/journal.pbio.0060033

Fournier, D., Skaug, H., Ancheta, J., Ianelli, J., Magnusson, A., Maunder, M., Nielsen, A. & Sibert, J. (2012). AD Model Builder: using automatic differentiation for statistical inference of highly parameterized complex nonlinear models. *Optimization Methods and Software*, **27**, pp. 233-249

Fox, J. (2003). Effect Displays in R for generalised linear models. *Journal of Statistical Software* **8**, 1-27. doi: 10.2307/271037

Fulton, T. W. (1904). The rate of growth of fishes. 22nd *Annual Report of the Fisheries Board of Scotland* **1903**, 141–241.

Gargan, P., Forde, G., Hazon, N., Russell, D. & Todd, C. (2012). Evidence for salmon lice induced marine mortality of Atlantic salmon (*Salmo salar*) in western Ireland from experimental releases of ranched smolts treated with emamectin benzoate. *Canadian Journal of Fisheries and Aquatic Sciences* **353**, 343-353. doi: 10.1139/F2011-155

Gauld, N., Campbell, R. & Lucas, M. (2016). Salmon and sea trout spawning migration in the River Tweed: telemetry derived insights for management. *Hydrobiologia* **767**, 111-123. doi: 10.1007/s10750-015-2481-0

Gillibrand, P. & Willis, K. (2007). Dispersal of sea louse larvae from salmon farms: modelling the influence of environmental conditions and larval behaviour. *Aquatic Biology* **1,** 63-75. 10.3354/ab00006

Gjelland, K., Serra-Llinares, R., Hedger, R., Arechavala-Lopez, P., Nilsen, R., Finstad, B., Uglem, I., Skilbrei, O. & Bjørn, P. (2014). Effects of salmon lice infection on the behaviour of sea trout in the marine phase. *Aquaculture Environment Interactions* **5**, 221-233. doi: 10.1007/s10750-015-2481-0

Glover, K., Solberg, M., McGinnity, P., Hindar, K., Verspooor, E., Coulson, M., Hansen, M., Araki, H., Skaala, Ø. & Svåsand, T. (2017). Half a century of genetic interaction between farmed and wild Atlantic salmon: status of knowledge and unanswered questions. *Fish and Fisheries* **18,** 890-927. doi: 10.1111/faf.12214

Gross, M., Coleman, R. & McDowal, R. (1988). Aquatic productivity and the evolution of diadromous fish migration. *Science* **239**, 1291-1293. doi: 10.1126/science.239.4845.1291

Hothorn, T., Bretz, F. & Westfall, P. (2008). Simultaneous inference in general parametric models. *Biometrical Journal* **50**, 346-363

ICES (2017*a*). Report of the workshop on sea trout 2 (WKTrutta2), ICES CM 2016/SSGEPD:20. Copenhagen: International Council for the Exploration of the Sea. Available at www.ices.dk/sites/pub/Publication%20Reports/Expert%20Group%20Report/SSGEPD/2016/01%20WKTRUTTA2%20-%20Report%20of%20the%20Workshop%20on%20Sea%20Trout%202.pdf

ICES (2017*b*). Report of the Working Group on North Atlantic Salmon (WGNAS). ICES CM 2017/ACOM:20. Copenhagen: International Council for the Exploration of the Sea. Available at http://ices.dk/sites/pub/Publication%20Reports/Expert%20Group%20Report/acom/2017/WGNAS/wgnas_2017.pdf

Jansen, P., Kristoffersen, A., Viljugrein, H., Jimenez, D., Aldrin, M. & Stien, A. (2012). Salmon lice as a density-dependent constraint to salmon farming. *Proceedings of the Royal Society B* **279**, 2330-2338. doi: 10.1098/rspb.2012.0084

Jennings, S., Stentiford, G., Leocadio, A., Jeffery, K., Metcalfe, J., Katsiadaki, I., Auchterlonie, N., Mangi, S., Pinnegar, J., Ellish, T., Peller, E., Luisetti, T., Baker-Austin, C., Brown, M., Catchpole, T., Clyne, F., Dye, S., Edmonds, N., Hyder, K.,

Lee, J., Lees, D., Morgan, O., O'Brien, C., Oidtmann, B., Posen, P., Santos, A., Taylor, N., Turner, A., Townhill, B. & Verner-Jefferys, D. (2016). Aquatic food security: insights into challenges and solutions from an analysis of interactions between fisheries, aquaculture, food safety, human health, fish and human welfare, economy and environment. *Fish and Fisheries* **17**, 1-46. doi: 10.1111/faf.12152

Jonsson B. & Jonsson N. (Eds) (2011). *Ecology of Atlantic Salmon and Brown Trout – Habitat as a Template for Life Histories*. *Fish and Fisheries Series* **33**. Dordrecht: Springer. doi: 10.1007/978-94-007-1189-1

Kenyon, W. & Davies, D. (2018). Salmon Farming in Scotland, S*P* 18-12 rev. Briefing prepared by the Scottish Parliament Information Centre for the Scottish Parliament Environment Climate Change and Land Resources Committee. Available at www.sp-bpr-en-prod-cdnep.azureedge.net/published/2018/2/13/Salmon-Farming-in-Scotland/SB%2018-12%20rev.pdf

Krkošek, M., Lewis, M. & Volpe, J. (2005). Transmission dynamics of parasitic sea lice from farm to wild salmon. *Proceedings of the Royal Society B* **272**, 689-696. doi: 10.1098/rspb.2004.3027

Limburg, K. & Waldman, J. (2009). Dramatic declines in North Atlantic diadromous fishes. *BioScience* **59**, 955-965. doi: 10.1525/bio.2009.59.11.7

Mazerolle, M. (2016). AICcmodavg: model selection and multimodel inference based on (Q)AIC(c). R package version 2.1-0. Available at https://cran.r-project.org/package=AICcmodavg

Middlemas, S., Fryer, R., Tulett, D. & Armstrong, A. (2013). Relationship between salmon lice levels on sea trout and fish farm activity in western Scotland. *Fisheries Management and Ecology* **20**, 68-74. doi: 10.1111/fme.12010

Nash, R., Valencia, A. Geffen, A. (2006). The origin of Fulton's condition factor – setting the record straight. *Fisheries* **5**, 236-238. doi: 10.1016/j.anbehav.2015.04.024

OECD (2018). Organisation for Economic Co-operation and Development. Aquaculture development. Available at www.stats.oecd.org/viewhtml.aspx?datasetcode+FISH_AQUA&lang=en

Parker, R. & Margolis, L. (1964). A new species of parasitic copepod, *Caligus clemensi* sp. nov. (*Caligoida: Caligidae*), from pelagic fishes in the coastal waters of British Columbia. *Journal of the Fisheries Research Board of Canada* **21,** 873-889. doi: 10.1139/f64-085

Penston, M., Millar, C., Zuur, A. & Davies, I. (2008). Spatial and temporal distribution of *Lepeophtheirus salmonis* (Krøyer) larvae in a sea loch containing Atlantic salmon, *Salmo salar* L., farms on the north-west coast of Scotland. *Journal of Fish Diseases* **31**, 361-371. doi: 10.1111/j.1365-2761.2008.00915.x

Penston, M. & Davies, I. (2009). An assessment of salmon farms and wild salmonids as sources of *Lepeophtheirus salmonis* (Krøyer) copepodids in the water column in Loch Torridon, Scotland. *Journal of Fish Diseases* **32**, 75-88. doi: 10.1111/j.1365-2761.2008.00986.x

Rae, G. (2002). Sea louse control in Scotland, past and present. *Pest Management Science* **58,** 515-520. doi: 10.1002/ps.491

Rees, E., St-Hilaire, S., Jones, S., Krkosek, M., DeDominicis, S., Foreman, M., Patanasatienkul, T. & Revie, C. (2015). Spatial patterns of sea lice infection among wild and captive salmon in western Canada. *Landscape Ecology* **30**, 989-1004. doi: 10.1007/s10980-015-0188-2

Salama, N., Collin, C., Fraser, J., Dunn, J., Pert, C., Murray, A. & Rabe, B. (2013). Development and assessment of a biophysical dispersal model for salmon lice. *Journal of Fish Diseases* **36**, 323-337. doi: 10.1111/jfd.12065

Sarkar, D. (2008). *Lattice: Multivariate Data Visualization with R*. New York, NY: Springer.

Scottish Government (2018). Scotland's Aquaculture. Available at www.aquaculture.scotland.gov.uk

Shephard, S., MacIntyre, C. & Gargan, P. (2016). Aquaculture and environmental drivers of salmon lice infestation and body condition in sea trout. *Aquaculture Environment Interactions* **8**, 597-610. doi: 10.3354/aei00201

Taranger, G., Karlsen, Ø., Bannister, R., Glover, K., Husa, V., Karlsbakk, E., Kvamme, B., Boxaspen, K., Bjørn, P., Finstad, B., Madhun, A., Morton, H. & Svåsand. T. (2015). Risk assessment of the environmental impact of Norwegian Atlantic salmon farming. *ICES Journal of Marine Science* **72**, 997-1021. doi: 10.1093/icesjms/fsu132

Thorstad, E., Todd, C., Uglem, I., Bjørn, P., Gargan, P., Vollset, K., Halttunen, E., Kålås, S., Berg, M. & Finstad, B. (2015). Effects of salmon lice *Lepeophtheirus salmonis* on wild sea trout *Salmo trutta* – a literature review. *Aquaculture Environment Interactions* **7**, 91-113. doi: 10.3354/aei00142

Thorstad, E., Todd, C., Uglem, I., Bjørn, P., Gargan, P., Vollset, K., Halttunen, E., Kålås, S., Berg, M. & Finstad, B. (2016). Marine life of the sea trout. *Marine Biology* **163**, 1-19. doi: 10.3354/aei00142

Tucker, C., Sommerville, C. & Wootten, R. (2002). Does size really matter? Effects of fish surface area on the settlement and initial survival of *Lepeophtheirus salmonis*, an ectoparasite of Atlantic salmon *Salmo salar*. *Diseases of Aquatic Organisms* **49,** 135-152. doi: 10.3354/dao049145

Urquhart, K., Pert, C., Fryer, R., Cook, P., Weir, S., Kilburn, R., McCarthy, U., Simons, J., McBeath, S., Matejusova, I., Bricknell, I. (2010). A survey on pathogens and metazoan parasites on wild sea trout (*Salmo trutta*) in Scottish waters. *ICES Journal of Marine Science* **67,** 444-453. doi: 10.1093/icesjms/fsp271

Wickham, H. (2009). *ggplot2: Elegant Graphics for Data Analysis*. New York, NY: Springer.

Wickham, H. (2011). The Split-Apply-Combine Strategy for Data Analysis. *Journal of Statistical Software*, **40**, 1-29. doi: 10.18637/jss.v040.i01

Zeileis, A., Kleiber, C. and Jackman, S. (2008). Regression Models for Count Data in R. *Journal of Statistical Software* **27**, 1-25. doi: 10.18637/jss.v027.i08

Zuur, A. and Ieno, E. (2016). *Beginner's Guide to Zero-Inflated Models with R*. Newburgh: Highland Statistics Ltd.

FIGURE CAPTIONS

FIG. 1. Maps of Isle of Skye and U.K. showing location of reference fish farms (▲) and sampling sites (●): 1, Loch Snizort; 2, Loch Portree; 3, Loch Harport; 4, Loch Slapin; Loch 5, Loch Eishort.

FIG. 2. A probability distribution curve depicting the significant correlation ($P < 0.001$) between the proximity (D) of *Salmo salar* farms and the likelihood of *Lepeophtheirus salmonis* presence. O, Uninfected fish present; ●, infected fish present.

FIG. 3. A probability distribution curve depicting the significant correlation ($P < 0.001$) between *Salmo trutta* fork length (L_F) and the likelihood of *Lepeophtheirus salmonis* presence. O, Uninfected fish at given length; ●, infected fish at given length.

FIG. 4. The significant correlation ($P < 0.05$) identified by a hurdle model between total *Lepeophtheirus salmonis* abundance found on *Salmo trutta* when *L. salmonis* abundance > 0 and the proximity (D) of the captured fish to the nearest *Salmo salar* farm. ▮, ± S.E.

FIG. 5. The proportions of different *Lepeophtheirus salmonis* life stages contributing to total lice abundance on *Salmo trutta* in relation to *Salmo salar* farm proximity (D). — —, Gravid female; • • •, juvenile; - • -, mobile.

FIG. 6. The significant interaction between total *Lepeophtheirus salmonis* abundance and the proximity (D) of a *Salmo salar* farm and their effects on the proportion of juvenile *L. salmonis* in the total sample of lice (N). ▌, Location of fish farm.

LIST OF FIGURES

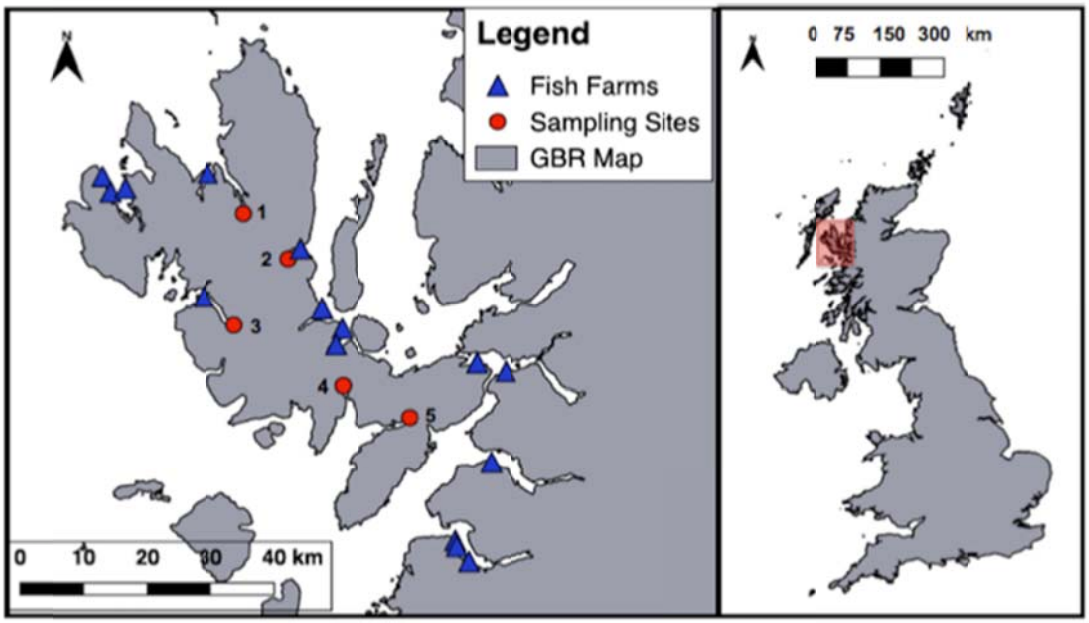

Figure 1.

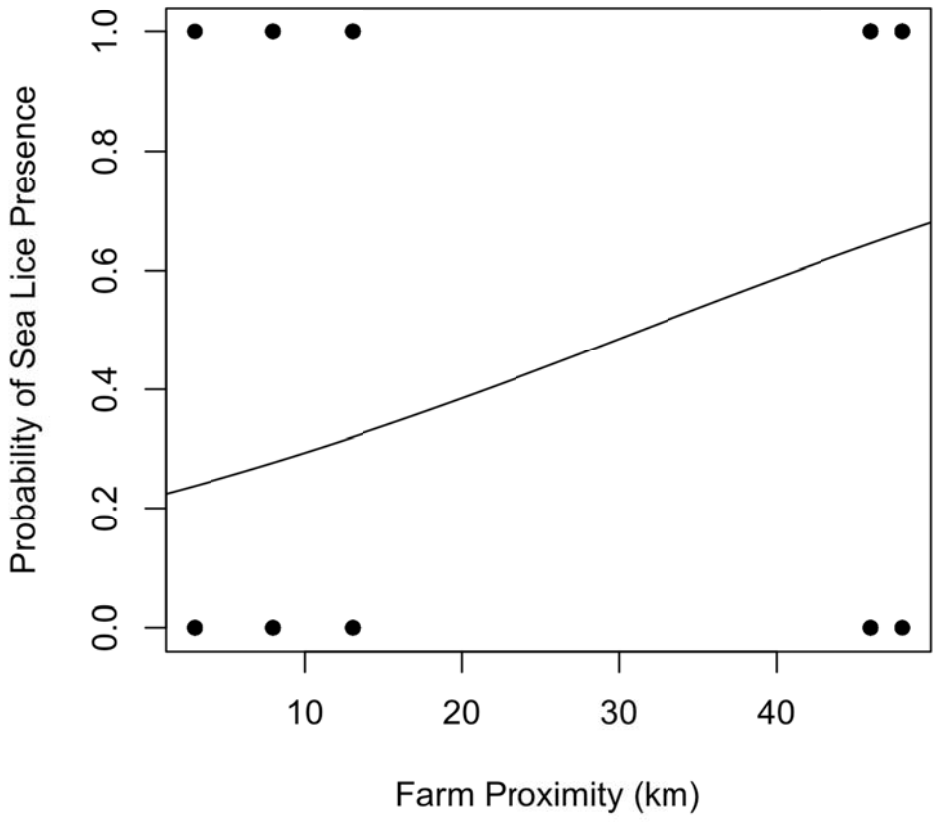

Figure 2

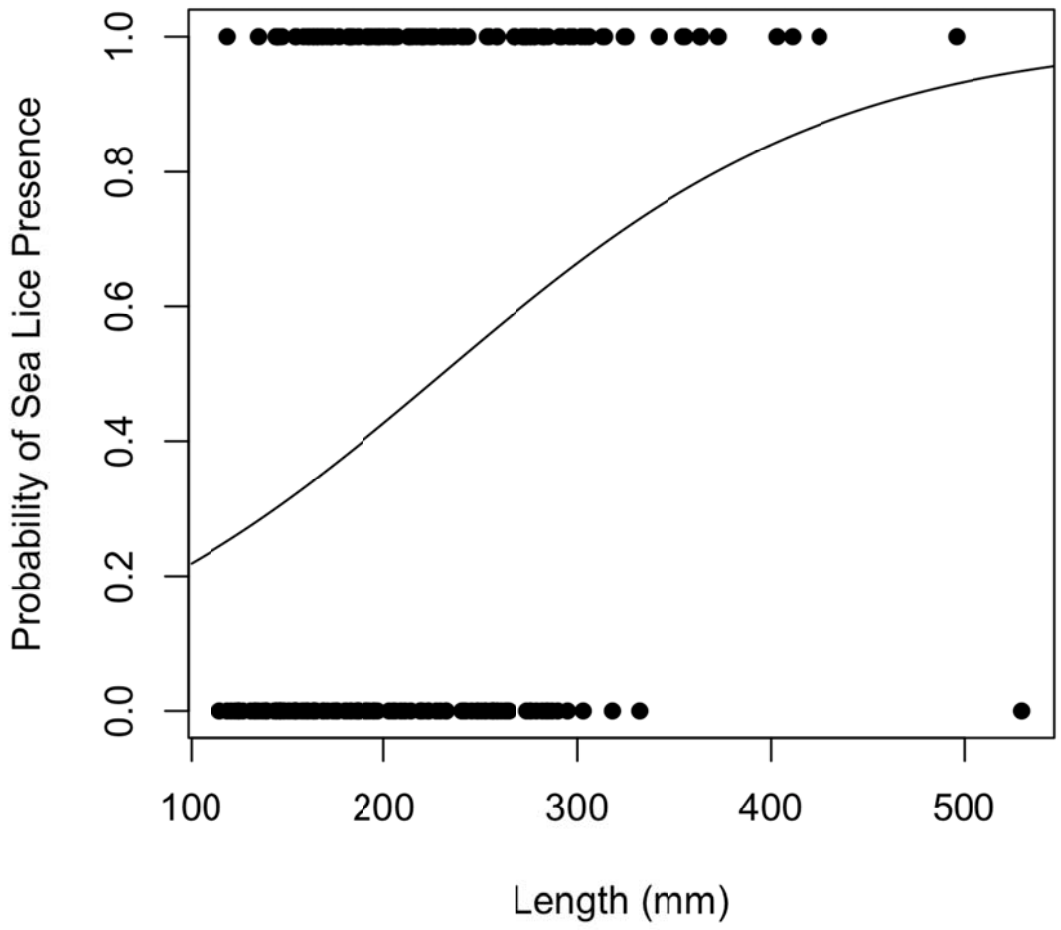

Figure 3.

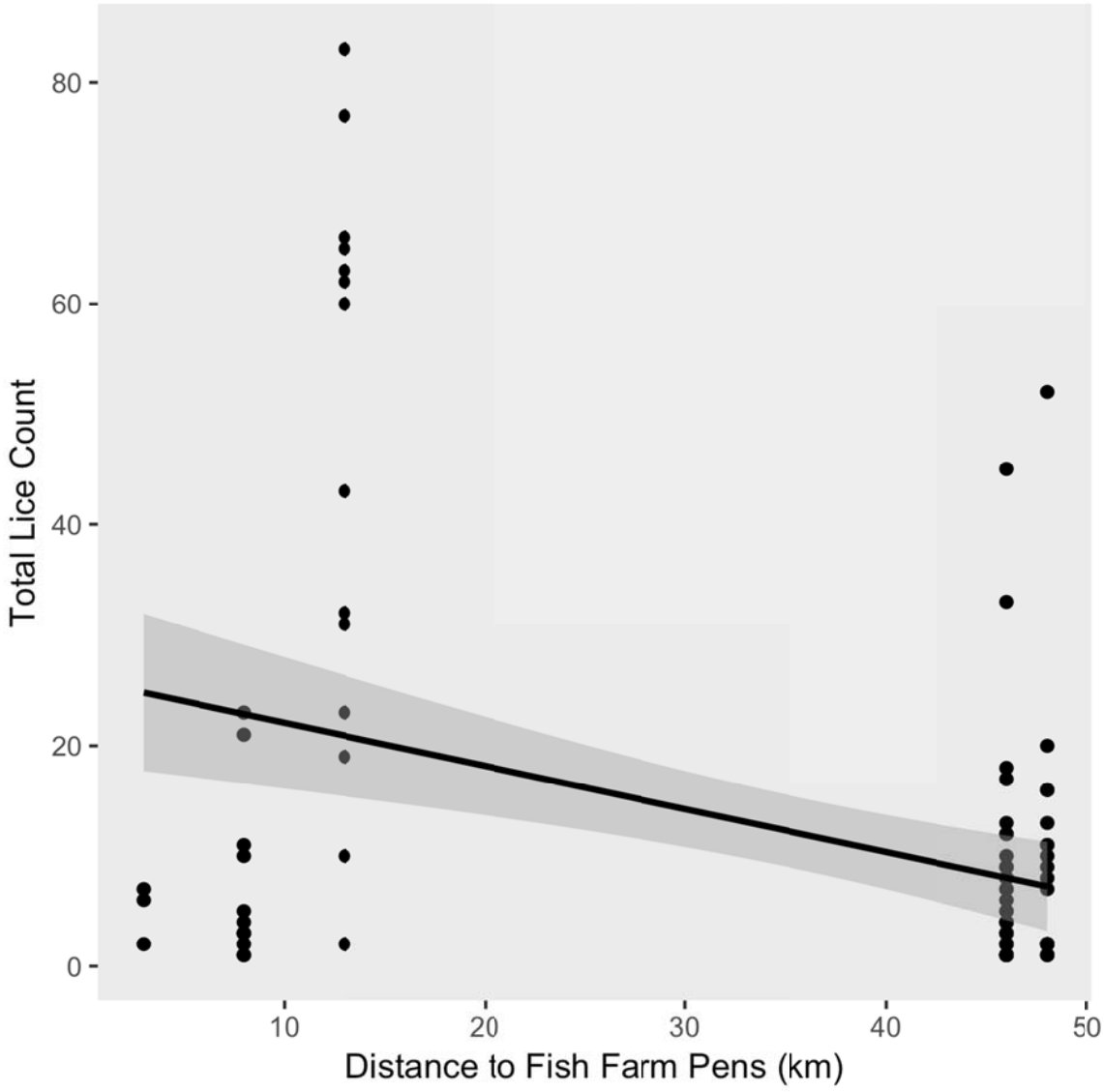

Figure 4.

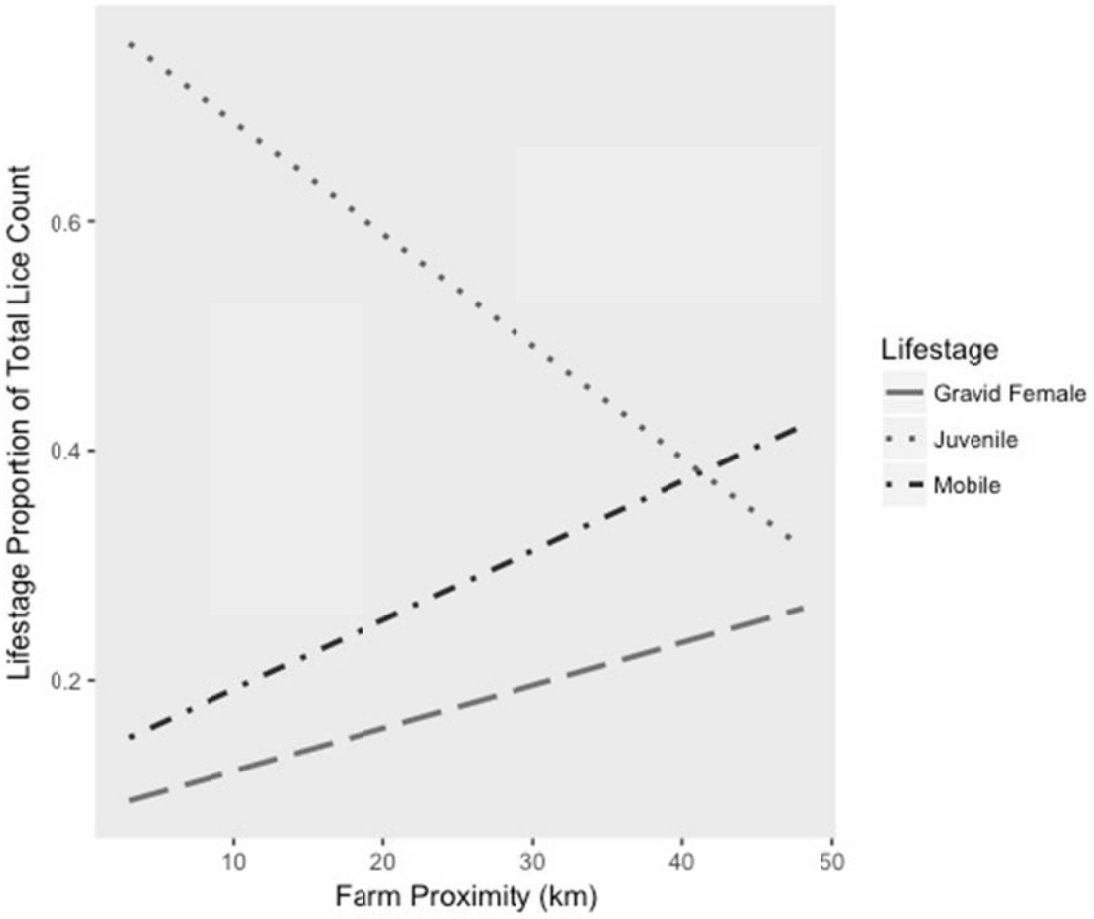

Figure 5.

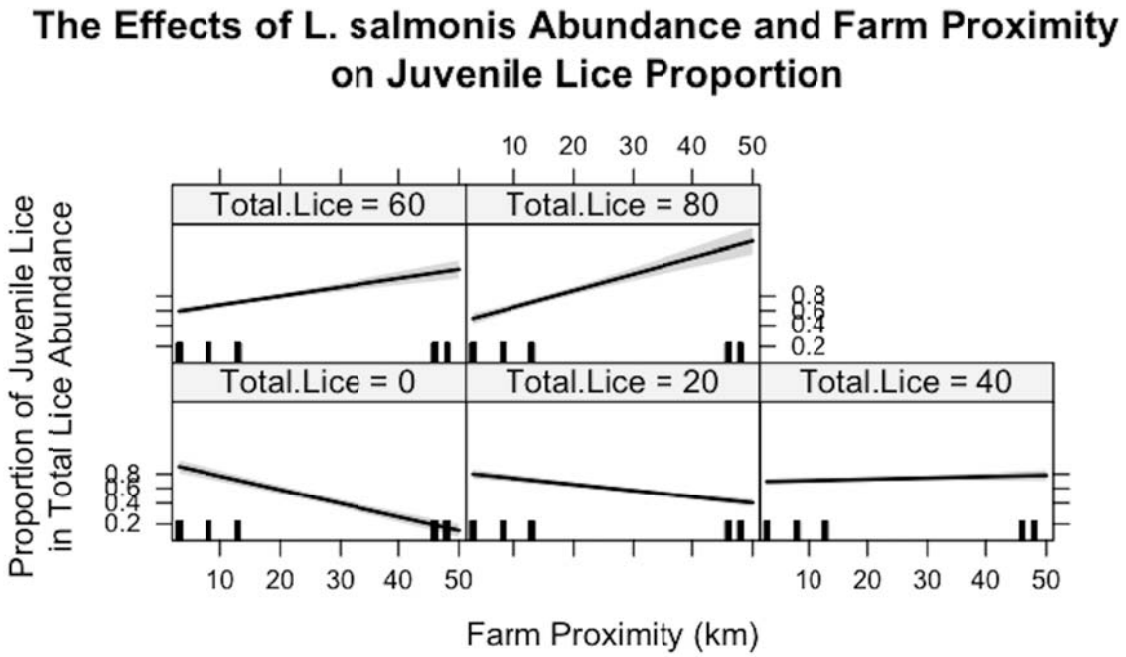

Figure 6.

LIST OF TABLES

TABLE I. The locations of the five sea lochs, their surface area (*A*), the type of capture netting method used at each site, the proximity of the site to the nearest active *Salmo salar* farm (*D*), the number of *Salmo trutta* caught (*n*) and fork length (L_F), and lice counts of *Lepeophtheirus salmonis* (juvenile, mobile, gravid female, and total lice) observed at each site

Sampling locations				*A*	Capture	*D*		L_F	Juvenile lice	Mobile lice	Gravid ♀lice	Total lice
Loch	River	N°	W°	(km^2)	netting	(km)	*n*	(mean ± S.E., mm)	(mean ± S.E)	(mean ± S.E)	(mean ± S.E)	(mean ± S.E)
Harport	Drynoch	57.29785	–6.31144	5	Fyke	8	36	217.7 ± 10.5	2.1 ± 0.9	0.2 ± 0.1	0.2 ± 0.1	2.5 ± 0.9
Eishort	Eishort	57.18780	–5.84029	5	Fkye	48	27	236.3 ± 11.2	3.0 ± 1.8	1.7 ± 0.4	2.3 ± 0.6	7.0 ± 2.1
Slapin	Strathmor	57.22107	–6.03199	7	Seine	46	88	227.8 ± 8.5	1.5 ± 0.5	1.3 ± 0.2	0.8 ± 0.2	3.7 ± 0.7
Snizort	Snizort	57.45962	–6.32072	9	Seine	13	31	165.7 ± 5.1	15.0 ± 3.8	5.2 ± 1.8	0.4 ± 0.2	20.5 ± 5.1
Portree	Varagill	57.39053	–6.20172	3	Fyke	3	44	216.1 ± 10.0	0.1 ± 0.1	0.1 ± 0.1	0.1 ± 0.1	0.3 ± 0.2
			All Sites				230	216.4 ± 4.6	3.4 ± 0.7	1.5 ± 0.3	0.7 ± 0.1	5.6 ± 0.9

TABLE II. Results from mixed-effects model identifying significant correlations between zero inflated *Lepeophtheirus salmonis* count data and the fork length (L_F) of *Salmo trutta* hosts and their proximity (D) to *Salmo salar* farms

	Estimate (S.E.)	Z	P
Binomial			
Intercept	–0.156 (0.150)	–1.041	> 0.05
D (km)	0.771 (0.151)	5.12	< 0.001
L_F (mm)	0.648 (0.174)	3.725	< 0.001
Truncated negative binomial			
Intercept	3.524 (0.394)	8.95	< 0.001
D (km)	–0.022 (0.007)	–3.06	< 0.01
L_F (mm)	–0.002 (0.001)	–1.42	> 0.05

TABLE II. General linear model output demonstrating how the proportion of various *Lepeophtheirus salmonis* life stages on *Salmo trutta* is significantly correlated to the host's proximity to the nearest fish farm (*D*) and to the total number of *L. salmonis* on *S. trutta* hosts

	Estimate (S.E.)	*Z*	*P*
Proportion of juvenile lice			
Intercept	–0.925 (0.143)	6.468	> 0.05
D (km): total lice (*n*)	0.001 (0.000)	–11.129	< 0.001
D (km)	–0.053 (0.138)	–0.005	< 0.001
Total lice	–0.019 (0.003)	–6.57	< 0.001
Proportion of mobile lice			
Intercept	–1.461 (0.106)	–13.755	< 0.001
D (km)	0.011 (0.003)	3.651	< 0.001
Proportion of gravid female lice			
Intercept	–0.925 (0.143)	–6.122	< 0.001
D (km)	0.031 (0.007)	4.689	< 0.001
Total lice	–0.049 (0.006)	–7.546	< 0.001